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Decomposition of beech leaf litter by Microflora and Mesofauna. II. Food preferences and action of oribatid mites on different substrates

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Abstract

The food preferences and the decomposing activity of three oribatid mites, *Steganacarus magnus*, *Achipteria coleoptrata* and *Damaeus verticillipes*, were studied using twelve different substrates, ranging from not decomposed beech leaves, to beech leaves that were partially decomposed by two white-rot fungi (Basidiomycetes), *Sporotrichum pulverulentum* (strain SPU) and one species from Fontainebleau Forest (strain FTS). In addition, one group of leaves was bleached chemically. The main differential food preferences were as follows: A) *S. magnus* – 1) beech litter bleached during 16 hours by NaClO; 2) beech litter decomposed during one month by FTS; 3) beech litter decomposed during one week by FTS; B) *A. coleoptrata* – 1) cellulose + polyphenols; 2) mycelium SPU; 3) beech litter not decomposed; 4) beech litter decomposed during one week by SPU; C) *D. verticillipes* – 1) mycelium FTS; 2) beech litter decomposed during one month by SPU. It should be noted that the oribatid preferences for the fungi (mycelium) were, in two out of three species, different from their preferential action on the leaves decomposed by the same fungi. Furthermore, and in conclusion, the association between oribatid mites and white-rot fungi increased the consumption rate of the beech leaves (litter) and, in that way, their rate of decomposition.

Keywords: Oribatid mites, white-rot fungi, beech litter, food preferences.

Résumé

Décomposition des litières de hêtre par la Microflore et la Mésofaune. II. Préférences alimentaires et action d'acariens oribates sur différents substrats.

Les préférences alimentaires et l'activité de décomposition de trois espèces d'acariens oribates, *Steganacarus magnus*, *Achipteria coleoptrata* et *Damaeus verticillipes*, ont été étudiées sur douze substrats différents allant des feuilles de hêtre non décomposées aux feuilles de hêtre partiellement décomposées par deux champignons de pourriture blanche (Basidiomycètes), *Sporotrichum pulverulentum* (souche SPU) et une espèce provenant de la Forêt de Fontainebleau (souche FTS). Par ailleurs, un groupe de feuilles a été décoloré chimiquement. Les principales préférences alimentaires différenciant les trois espèces furent les suivantes : A) *S. magnus* – 1) feuilles de hêtre décolorées pendant 16 heures par NaClO ; 2) feuilles de hêtre décomposées pendant un mois par FTS ; 3) feuilles de hêtre décomposées pendant une semaine par FTS ; B) *A. coleoptrata* – 1) cellulose + polyphénols ; 2) mycélium de SPU ; 3) feuilles de hêtre non décomposées ; 4) feuilles de hêtre décomposées pendant une semaine par SPU ; C) *D. verticillipes* – 1) mycélium de FTS ; 2) feuilles de hêtre décomposées pendant un mois par SPU. Il est remarquable que les préférences des oribates pour les champignons (mycélium) ont été, en deux cas sur trois, différentes de leurs préférences pour les feuilles décomposées par les mêmes champignons. Par ailleurs, et en conclusion, l'association entre les acariens oribates et les champignons de pourriture blanche augmente le taux de consommation des feuilles de hêtre (litière), et, de ce fait, leur taux de décomposition.

Mots-clés : Acariens oribates, champignons de pourriture blanche, litière de hêtre, préférences alimentaires.

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INTRODUCTION

The main functions of soil microarthropods as decomposers are classically the comminution of the organic matter (litter), the control of the development of the microorganisms and their dispersal. In any case, this function is related to the trophic behaviour of these microarthropods and their effects on the decomposition processes (Behan & Hill, 1978; Cancela da Fonseca & Poinsot-Balaguer, 1983; Siepel, 1994).

Since the reviews of Petersen & Luxton (1982) and Cancela da Fonseca & Poinsot-Balaguer (1983) on the feeding habits of microarthropods several papers were published on the same subject (e.g. among others; Behan-Pelletier & Hill, 1983; Mittmann, 1983; Rohrer & Reutimann, 1984; Norton, 1985; Usher, 1985; Visser, 1985; Reutimann, 1987; Walter, 1987; Hågvar, 1988; Kaneko, 1988; Saur & Ponge, 1988; Siepel, 1990; Walsh & Bolger, 1990; Leonard & Anderson, 1991; Webb, 1991; Siepel & de Ruiter-Dijkman, 1993; Siepel, 1994; Siepel & Maaskamp, 1994).

Most of them concerned the food preferences and some the ability of the microarthropods to digest the food available.

On the grounds of food preferences and enzyme complexes Schuster (1956) and Luxton (1972) defined three main categories of microarthropods: macrophytophages (feeding on higher plant material), microphytophages (feeding on microflora) and panphytophages (feeding on both plant material and microflora). To this classification followed that of Siepel & de Ruiter-Dijkman (1993) based on the enzymatic activity of three carbohydrases: cellulase, chitinase and trehalase. Five main feeding guilds were set forth: herbivorous grazers (cellulase activity only), herbivorous browsers (absence of the three enzymes activity), fungivorous grazers (chitinase activity as well as trehalase activity), fungivorous browsers (trehalase activity only), and herbofungivorous grazers (the three enzymes activity). The macrophytophages become then herbivorous grazers and browsers; the microphytophages, fungivorous grazers and browsers; and, the panphytophages, herbofungivorous grazers.

As Cancela da Fonseca & Poinsot-Balaguer (1983) suggested, we were interested to get further in the analysis of the feeding preferences of oribatid mites, mainly in relation with the white-rot fungi predominant in our beech forest. Thus, a double experimental work was done. First, to study the action of three strains of white-rot fungi (Basidiomycetes) on the decomposition of beech litter (*Fagus sylvatica* L.) (Rihani *et al.*, in press): loss of weight, bleaching, losses of cellulose, lignin and phenolic compounds were measured. The most active fungus was *Sporotrichum pulverulentum* Nov., whose rates of degradation reached about 75%, followed by the two unidentified species, strains RM and FTS.

Second, to study the decomposing activity of three species of oribatid mites present in the same beech woodland as the white-rot fungi, through their food preferences, to evaluate their relative role on the maintenance of the natural fertility of forest soil.

MATERIAL AND METHODS

The three species of oribatid mites studied were: *Steganacarus magnus* (Nic.) (macrophytophage), *Achipteria coleoptrata* (L.) (panphytophage), and *Damaeus verticillipes* Nic. (microphytophage). They are beech litter species and came from a beech woodland, Fontainebleau Forest. From the same forest, particularly from the soil of La Tillaie Biological Reserve, the white-rot fungus F.T.S. (strain FTS) was isolated. The other lignivore fungus utilised in the experiments was *S. pulverulentum* (SPU; strain CBS.481.73).

Twelve substrates (food material) were given separately to the three oribatid species. They were:

S01 (FSY) = Control: beech litter (leaves) not decomposed;

S02 (cellulose) = Cellulose fibers: filter paper;

S03 (polyphenols) = Cellulose fibers: filter paper saturated with polyphenols extracted by methanol from undecomposed beech leaves;

S04 (lignin) = Lignin of Klason: 3 mg on a disc of glass-fiber filter paper;

S05 (FTS) = Mycelium of FTS on a disc of glass-fiber filter paper, previously placed on a malt-agar culture of these fungi;

S06 (SPU) = Mycelium of SPU on a disc of glass-fiber filter paper, previously placed on a malt-agar culture of these fungi;

S07 (FSY + FTS:1w) = Beech litter (leaves) decomposed during one week by FTS;

S08 (FSY + FTS:1m) = Beech litter (leaves) decomposed during one month by FTS;

S09 (FSY + SPU:1w) = Beech litter (leaves) decomposed during one week by SPU;

S10 (FSY + SPU:1m) = Beech litter (leaves) decomposed during one month by SPU;

S11 (FSY + NaClO:2 h) = Beech litter (leaves) bleached during 2 hours by sodium hypochlorite: NaClO 12° Chl.;

S12 (FSY + NaClO:16 h) = Beech litter (leaves) bleached during 16 hours by sodium hypochlorite: NaClO 12° Chl.

The experimental conditions were as follows: (a) The mites were reared at the temperature of 22°C and R.H. of about 95%; (b) For each substrate and each species, 3 replicates were applied, *i.e.* 3 boxes of plaster of Paris + charcoal covered with a disc of glass-fiber filter paper (Goto, 1961), their cap having a hole closed by a 42 μm mesh nylon net; (c) In each box 3 discs (∅12 mm; average 4.9 mg dry weight) of

the same food material and 10 adult mites, deprived of their original forest food for four days, were placed; (d) At the start of the experiments (control discs) and one week, one month and three months later the dry weight of the substrates was measured.

Quantitative analysis of the data was done using: (a) the paired *t*-test, to evaluate the significance of the differences between two feeding rates; (b) the sign test, to evaluate if the rates of food consumption of a set of data are significantly different of another set,

Table 1. – Quantity of food material consumed by *Steganacarus magnus* after 1 week, 1 month and 3 months of culture in the laboratory. (Mean in % of initial dry weight ± standard deviation.)

Food material	1 week	1 month	3 months
S01 (FSY)	1.64 ± 1.27	9.70 ± 1.80	13.20 ± 1.90
S02 (cellulose)	2.20 ± 0.70	7.50 ± 0.50	13.60 ± 1.20
S03 (polyphenols)	0.87 ± 0.05	3.10 ± 1.10	8.20 ± 0.60
S04 (lignin)	...	1.50 ± 0.40	...
S05 (FTS)	0.49 ± 0.20	3.45 ± 0.52	...
S06 (SPU)	1.30 ± 0.20	4.40 ± 0.60	6.76 ± 0.74
S07 (FSY + FTS:1w)	1.27 ± 0.09	13.00 ± 0.61	21.10 ± 1.40
S08 (FSY + FTS:1m)	4.45 ± 0.48	18.70 ± 0.68	23.50 ± 0.69
S09 (FSY + SPU:1w)	1.49 ± 0.08	9.96 ± 0.30	15.00 ± 0.48
S10 (FSY + SPU:1m)	1.04 ± 0.12	10.40 ± 0.24	11.80 ± 0.47
S11 (FSY + NaClO:2 h)	2.11 ± 0.29	10.50 ± 0.55	14.40 ± 0.89
S12 (FSY + NaClO:16 h)	5.74 ± 0.40	21.40 ± 1.07	30.10 ± 0.74

... No measurements were made.

Table 2. – Quantity of food material consumed by *Achipteria coleoptrata* after 1 week, 1 month and 3 months of culture in the laboratory. (Mean in % of initial dry weight ± standard deviation.)

Food material	1 week	1 month	3 months
S01 (FSY)	2.37 ± 1.70	20.20 ± 4.30	25.10 ± 2.10
S02 (cellulose)	4.43 ± 0.54	20.30 ± 1.50	26.00 ± 1.30
S03 (polyphenols)	5.06 ± 0.74	22.30 ± 1.80	24.80 ± 1.30
S04 (lignin)	...	8.50 ± 1.60	...
S05 (FTS)	1.25 ± 0.17	8.40 ± 0.60	...
S06 (SPU)	3.20 ± 0.20	11.40 ± 1.20	17.00 ± 1.10
S07 (FSY + FTS:1w)	3.30 ± 0.36	11.50 ± 0.58	15.40 ± 0.76
S08 (FSY + FTS:1m)	3.50 ± 0.50	13.10 ± 0.40	17.40 ± 0.50
S09 (FSY + SPU:1w)	2.57 ± 0.39	13.20 ± 0.44	17.30 ± 0.26
S10 (FSY + SPU:1m)	2.35 ± 0.25	9.35 ± 0.41	12.00 ± 0.20
S11 (FSY + NaClO:2 h)	2.63 ± 0.55	16.10 ± 1.09	18.60 ± 0.48
S12 (FSY + NaClO:16 h)	3.15 ± 0.63	18.80 ± 0.90	22.20 ± 0.70

... No measurements were made.

Table 3. – Quantity of food material consumed by *Damaeus verticillipes* after 1 week, 1 month and 3 months of culture in the laboratory. (Mean in % of initial dry weight ± standard deviation.)

Food material	1 week	1 month	3 months
S01 (FSY)	0	1.94 ± 0.54	3.70 ± 1.05
S02 (cellulose)	...	...	...
S03 (polyphenols)	0	2.20 ± 0.50	3.85 ± 0.80
S04 (lignin)	...	...	...
S05 (FTS)	6.99 ± 1.08	13.20 ± 1.50	...
S06 (SPU)	4.96 ± 0.66	10.40 ± 0.68	11.20 ± 1.02
S07 (FSY + FTS:1w)	0.92 ± 0.13	5.74 ± 0.75	6.05 ± 0.28
S08 (FSY + FTS:1m)	2.77 ± 0.46	11.30 ± 1.02	...
S09 (FSY + SPU:1w)	4.04 ± 0.20	9.10 ± 1.00	11.30 ± 0.95
S10 (FSY + SPU:1m)	3.28 ± 0.33	12.50 ± 0.70	12.70 ± 0.60
S11 (FSY + NaClO:2 h)	0	1.50 ± 0.68	2.43 ± 0.90
S12 (FSY + NaClO:16 h)	0	2.53 ± 1.20	3.23 ± 0.38

... No measurements were made.

either time or species data (Siegel, 1956); and, (c) the correspondence analysis (ANAFAC), which gives the degree of statistical distance between variables (species), *i.e.* their relative importance expressed by their contributions (C1, C2,... in %) to the definition of each factor (axes Ax1, Ax2,...; for each factor the total sum of the contributions is 100%), and in relation with their significant differential attributes (food material) expressed also by their contributions to the definition of each factor (Benzécri & Benzécri, 1980).

RESULTS

A. Steganacarus magnus

The consumption of the leaves not attacked by the fungi (S01) was more or less stable after one month and did not differ significantly from the consumption of pure cellulose (S02), and the consumption of the leaves decomposed by SPU (S09, S10) or bleached by NaClO during two hours (S11) (*table* 1). On the other hand, the less consumed food materials were cellulose + polyphenols (S03), purified lignin (S04) and in general fungal mycelia (S05, S06), particularly the FTS one (S05) (*table* 1). However, *S. magnus* food preferences went mainly to the leaves bleached during 16 hours by NaClO (S12) and to the leaves decomposed by FTS, firstly during one month (S08) and secondly during one week (S07). In relation to the leaves not attacked by the fungi (S01), *S. magnus* clearly chose the leaves decomposed during one month by FTS (S08). These leaves were also preferred to those attacked during one month by SPU (S10); in both cases, about two times more (S10) (*table* 4).

The consumption rate per week decreased strongly after one month for all the substrates, but only for four of them after one week; slightly for the leaves bleached during 16 hours by NaClO (S12), the mycelium of SPU (S06) and the cellulose + polyphenols (S03), and more strongly for the pure cellulose (S02) (*table* 7 and *table* 8).

B. Achipteria coleoptrata

This species consumed mainly, at least after one week, cellulose + polyphenols (S03), pure cellulose (S02), leaves not attacked by the fungi (S01) as well as leaves bleached by NaClO either during 16 hours (S12) or two hours (S11), the differences in consumption being very small (*table* 2). Actually, this species seemed to prefer them to mycelium or to leaves already decomposed by the fungi. The food less preferred by *A. coleoptrata* was the mycelium of FTS (S05) and the purified lignin (S04). However, it preferred the mycelium of SPU (S06) and the leaves decomposed by FTS (S07, S08) and by SPU (S09, S10), the leaves decomposed by FTS being consumed in the first week about 1.5 times more than those decomposed by SPU (*table* 5).

As for *S. magnus*, the consumption rate per week decreased strongly after one month for all the substrates, but also for only four of them after one week, nevertheless not the same: slightly for the leaves decomposed during one month either by SPU (S10) or by FTS (S08), and more strongly for the leaves decomposed during one week by FTS (S07), and for the mycelium of SPU (S06) (*table* 7 and *table* 8).

C. Damaeus verticillipes

D. verticillipes consumed mainly the fungal mycelia or the leaves attacked by them (S05 to S10) (*table* 3). This consumption was much higher than that of the leaves not attacked by the fungi (S01) or attacked chemically by NaClO (S11, S12), and than that of the cellulose + polyphenols (S03); those leaves not being even slightly consumed during the first week (*table* 3). The species preference goes to the mycelium, particularly the FTS one (S05), followed by the SPU mycelium (S06), and the leaves decomposed by the latter, during one month (S10) and one week (S09) (*table* 6).

Again, the decomposition rate per week decreased after one month. It decreased also after one week for four substrates: slightly for the leaves decomposed during one month by SPU (S10), and more strongly for the leaves decomposed during one week by SPU (S09) and the mycelia of FTS (S05) and SPU (S06) (*table* 7 and *table* 8).

D. Comparison between the three species

The comparative analysis between the three species of Acari revealed some important differences, in terms of nutritional preferences (*table* 9; *fig.* 1).

Thus, the most characteristic preference of *S. magnus* was, firstly, its consumption of the beech leaves bleached by NaClO during 16 hours (S12) over that of *A. coleoptrata* (about 1.8 times more for the first week and 1.1 times for the first month), and mainly over that of *D. verticillipes* which is a microphytophage, not attracted by this type of leaves. Secondarily, it was characterised by its preference for the leaves decomposed by the fungus FTS during one week (S07) and one month (S08) over *D. verticillipes* (about respectively 1.4-2.3 and 1.6-1.7 times more) and one month (S08) over *A. coleoptrata* (about 1.3-1.4 times more).

A. coleoptrata seemed more versatile. Firstly, it preferred the not decomposed beech leaves (S01), mainly after one and three months of consumption (about twice that of *S. magnus*), and the cellulose + polyphenols (S03), particularly over *S. magnus* after one month of consumption (about 7 times more). *D. verticillipes* was not attracted by

Table 4. – Feeding ratios (> 1.0) of the food material consumed by *S. magnus* and their significant preferences. (E.g. - Feeding ratio = S01 feeding rate/S02 feeding rate; *table* 1.)

Food material	S01 (FSY)			S02 (cellulose)			S03 (polyphenols)			S05 (FTS)			S06 (SPU)			S07 (FSY + FTS:1w)			S08 (FSY + FTS:1m)			S09 (FSY + FTS:1m)			S10 (FSY + SPU:1m)			S11 (FSY + NaClO:2h)			S12 (FSY + NaClO:16h)		
	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m
S01	–	–	–	x	13	–	1.9	3.1*	1.6*	3.4	2.8*	–	1.3	2.2*	2.0*	1.3	x	x	x	x	x	1.1	x	x	1.6	x	1.1	x	x	x	x	x	x
S02	13	x	x	–	–	–	2.5	2.4*	1.7*	4.5	2.2*	–	1.7	1.7*	2.0*	1.7	x	x	x	x	x	1.5	x	x	2.1	x	1.2	x	x	x	x	x	x
S03	x	x	x	x	x	x	–	–	–	1.8	x	–	x	x	1.2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
S05	x	x	–	x	x	–	x	1.1	–	–	–	–	x	x	–	x	x	–	x	x	–	x	x	–	x	x	–	x	x	–	x	x	–
S06	x	x	x	x	x	x	1.5	1.4	x	2.7	1.3	–	–	–	–	x	x	x	x	x	x	x	x	x	1.3	x	x	x	x	x	x	x	x
S07	x	1.3	1.6*	x	1.7*	1.6*	1.5	4.2*	2.6*	2.6	3.8*	–	x	3.0*	3.1*	–	–	–	x	x	x	x	1.3	1.4	1.2	1.3	1.8*	x	1.2	1.5	x	x	x
S08	2.7	1.9*	1.8*	2.0	2.5*	1.7*	5.1*	6.0*	2.9*	9.1*	5.4*	–	3.4	4.3*	3.5*	3.5	1.4	1.1	–	–	–	3.0*	1.9*	1.6*	4.3*	1.8*	2.0*	2.1	1.8*	1.6*	x	x	x
S09	x	x	1.1	x	1.3	1.1	1.7	3.2*	1.8*	3.0	2.9*	–	1.2	2.3*	2.2*	1.2	x	x	x	x	x	–	–	–	1.4	x	1.3	x	x	x	x	x	x
S10	x	1.1	0.9	x	1.4	x	1.2	3.4*	1.4	2.1	3.0*	–	x	2.4*	1.8*	x	x	x	x	x	x	x	x	x	–	–	–	x	x	x	x	x	x
S11	1.3	1.1	1.1	x	1.4	1.1	2.4	3.4*	1.8*	4.3	3.0*	–	1.6	2.4*	2.1*	1.7	x	x	x	x	x	1.4	1.1	x	2.0	x	1.2	–	–	–	x	x	x
S12	3.5	2.2*	2.3*	2.6	2.9*	2.2*	6.6*	6.9*	3.7*	11.7*	6.2*	–	4.4*	4.9*	4.5*	4.5*	1.7*	1.4*	1.3	1.1	1.3*	3.9*	2.2*	2.0*	5.5*	2.1*	2.6*	2.7	2.0*	2.1*	–	–	–

a) 1w = 1 week, 1m = 1 month, 3m = 3 months of food consumption.

b) x: feeding ratios ≤ 1.0.

c) *: t-test: significant difference between two feeding rates at $p < 0.05$ (Rihani, 1988).

Table 5. – Feeding ratios (> 1.0) of the food material consumed by *A. coleoptrata* and their significant preferences. (E.g. - Feeding ratio = S01 feeding rate/S02 feeding rate; *table* 2.)

Food material	S01 (FSY)			S02 (cellulose)			S03 (polyphenols)			S05 (FTS)			S06 (SPU)			S07 (FSY + FTS:1w)			S08 (FSY + FTS:1m)			S09 (FSY + SPU:1m)			S10 (FSY + SPU:1m)			S11 (FSY + NaClO:2h)			S12 (FSY + NaClO:16h)		
	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m
S01	–	–	–	x	x	x	x	x	x	1.9	2.4*	–	x	1.8	1.5	x	1.8	1.6*	x	1.5	1.4	x	1.5	1.5	x	2.2*	2.1*	x	1.3	1.4	x	1.1	1.1
S02	1.9	x	x	–	–	–	x	x	1.1	3.5	2.4*	–	1.4	1.8*	1.5*	1.3	1.8*	1.7*	1.3	1.6	1.5*	1.7	1.5	1.5*	1.9	2.2*	2.2*	1.7	1.3	1.4	1.4	1.1	1.2
S03	2.1	1.1	x	1.1	1.1	x	–	–	–	4.1*	2.7*	–	1.6	2.0*	1.5	1.5	1.9*	1.6*	1.5	1.7*	1.4	2.0*	1.7*	1.4	2.2*	2.4*	2.1*	1.9*	1.4	1.3	1.6	1.2	1.1
S05	x	x	–	x	x	–	x	x	–	–	–	–	x	x	–	x	x	–	x	x	–	x	x	–	x	x	–	x	x	–	x	x	–
S06	1.4	x	x	x	x	x	x	x	x	2.6*	1.4	–	–	–	–	1.1	x	1.1	x	x	x	1.3	x	x	1.4	1.2	1.4*	1.2	x	x	x	x	x
S07	1.4	x	x	x	x	x	x	x	x	2.6*	1.4	–	x	x	x	–	–	–	x	x	x	1.3	x	x	1.4	1.2	1.3*	1.4	x	x	1.1	x	x
S08	1.5	x	x	x	x	x	x	x	x	2.8*	1.6	–	1.1	1.2	x	1.1	1.1	1.1	–	–	–	1.4	x	x	1.5	1.4*	1.5*	1.3	x	x	1.1	x	x
S09	1.1	x	x	x	x	x	x	x	x	2.1*	1.6*	–	x	1.2	x	x	1.2	1.1	x	x	x	–	–	–	1.1	1.4*	1.4*	x	x	x	x	x	x
S10	x	x	x	x	x	x	x	x	x	1.9*	1.1*	–	x	x	x	x	x	x	x	x	x	x	x	x	–	–	–	x	x	x	x	x	x
S11	1.1	x	x	x	x	x	x	x	x	2.1*	1.9*	–	x	1.4*	1.1	x	1.4*	1.2*	x	1.2*	1.1	x	1.2*	1.1	x	1.7*	1.6*	–	–	–	x	x	x
S12	1.3	x	x	x	x	x	x	x	x	2.5*	2.2*	–	x	1.7*	1.3*	x	1.6*	1.4*	x	1.4*	1.3*	1.2	1.4*	1.3*	1.3	2.0*	1.9*	1.2	1.2	1.2*	–	–	–

a) 1w = 1 week, 1m = 1 month, 3m = 3 months of food consumption.

b) x: feeding ratios ≤ 1.0.

c) *: t-test: significant difference between two feeding rates at $p < 0.05$ (Rihani, 1988).

Table 6. – Feeding ratios (> 1.0) of the food material consumed by *D. verticillipes* and their significant preferences. (E.g. - Feeding ratio = S01 feeding rate/S02 feeding rate; *table* 3.)

Food material	S01 (FSY)			S03 (polyphenols)			S05 (FTS)			S06 (SPU)			S07 (FSY + FTS:1w)			S08 (FSY + FTS:1m)			S09 (FSY + SPU:1w)			S10 (FSY + SPU:1m)			S11 (FSY + NaClO:2h)			S12 (FSY + NaClO:16h)		
	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m	1w	1m	3m
S01	–	–	–	x	x	x	x	x	–	x	x	x	x	x	x	x	x	–	x	x	x	x	x	x	x	1.3	1.5	x	x	1.2
S03	x	1.1	x	–	–	–	x	x	–	x	x	x	x	x	x	x	x	–	x	x	x	x	x	x	x	1.5	1.6	x	x	1.2
S05	∞*	6.8*	–	∞*	6.0*	–	–	–	–	1.4*	1.3*	–	7.6*	2.3*	–	2.5*	1.2	–	1.7*	1.5*	–	2.1*	1.1	–	∞*	8.8*	–	∞*	5.2*	–
S06	∞*	5.4*	3.0*	∞*	4.7*	2.9*	x	x	–	–	–	–	5.4*	1.8*	1.9*	1.8*	x	–	1.2	1.1	x	1.5	x	x	∞*	6.9*	4.6*	∞*	4.1*	3.5*
S07	∞*	3.0*	1.6*	∞*	2.6*	1.6*	x	x	–	x	x	x	–	–	–	x	x	–	x	x	x	x	x	x	∞*	3.8*	2.5*	∞*	2.3*	1.9*
S08	∞*	5.8*	–	∞*	5.1*	–	x	x	–	x	1.1	–	3.0*	2.0*	–	–	–	–	x	1.2	–	x	x	x	∞*	7.5*	–	∞*	4.5*	–
S09	∞*	4.7*	3.1*	∞*	4.1*	2.9*	x	x	–	x	x	x	4.4*	1.6*	1.9*	1.5*	x	–	–	–	–	1.2	x	x	∞*	6.1*	4.7*	∞*	3.6*	3.5*
S10	∞*	6.4*	3.4*	∞*	5.7*	3.3*	x	x	–	x	1.2	1.1	3.6*	2.2*	2.1*	1.2	1.1	–	x	1.4*	1.1	–	–	–	∞*	8.3*	5.2*	∞*	4.9*	3.9*
S11	x	x	x	x	x	x	x	x	–	x	x	x	x	x	x	x	x	–	x	x	x	x	x	x	–	–	–	x	x	x
S12	x	1.3	x	x	x	x	x	x	–	x	x	x	x	x	x	–	x	–	x	x	x	x	x	x	x	1.7	1.3	–	–	–

a) 1w = 1 week, 1m = 1 month, 3m = 3 months of food consumption.
b) x: feeding ratios ≤ 1.0.
c) ∞: Quotient X/0.
d) *: t-test: significant difference between two feeding rates at $p < 0.05$ (Rihani, 1988).

these substrates. In the second place, *A. coleoptrata* preferred the mycelium of FTS (S05) and of SPU (S06) over the preferences of *S. magnus*, mainly after one month of consumption (about 2.5 times more). It preferred even the mycelium of SPU (S06) over the preferences of *D. verticillipes*, also after one month of consumption. Thirdly, the beech leaves decomposed during one week either by FTS (S07) or by SPU (S09) were also preferred by *A. coleoptrata* in relation to the preferences of both *S. magnus* and *D. verticillipes*: (a) for leaves + FTS, respectively 2.6 times and 3.6 times after one week of consumption; (b) for leaves + SPU, respectively 1.3 times and 1.5 times after one month of consumption. It is also interesting to indicate that this species preferred, more than *S. magnus*, both the pure cellulose (S02) and the leaves bleached during two hours by NaClO (S11), mainly after one month consumption: respectively 2.7 and 1.5 times more.

As a microphytophage, the preferences of *D. verticillipes* were towards the mycelium of either FTS (S05) or SPU (S06), but mainly to that of FTS: about 14 and 4 times more than those of *S. magnus*, and 5.6 and 1.6 more than those of *A. coleoptrata* after one week and one month of consumption. The preference for the mycelium of SPU concerned principally the first week of consumption: 3.8 times more than that of *S. magnus* and 1.6 more than that of *A. coleoptrata*. The third interesting differential preference concerned the leaves decomposed during one month by SPU (S10) after one month and one week of consumption (1.2 and 3.2 times more than that of *S. magnus* and 1.3 and 1.4 times more than that of *A. coleoptrata*) and also to the leaves decomposed during one week by the same fungus (S09) (2.7 times more than *S. magnus* and 1.6 times more than *A. coleoptrata*).

During the first week and the first month, the feeding activity rate was in general higher for *A. coleoptrata* than for *S. magnus*. The main exceptions were the consumption of leaves decomposed during one month by FTS (S08) and the leaves bleached during 16 hours by NaClO (S12). In the second and third months, the rate decreased strongly, but it is, in general, slightly higher for *S. magnus*. On the contrary, during the first week, *D. verticillipes* had a feeding activity rate higher than those of *S. magnus* and *A. coleoptrata* concerning both the fungal mycelium (S05, S06) and the leaves decomposed by SPU (S09, S10). This rate decreased very strongly in the second and third months becoming much lower than those of the two other species.

DISCUSSION AND CONCLUSION

Though the general feeding preferences of *S. magnus*, *A. coleoptrata* and *D. verticillipes* are already known (Spencer, 1951; Murphy, 1952, 1953, 1954, 1955, 1957; Schuster, 1956; Wallwork, 1958; Hayes, 1963; Berthet, 1964; Farahat, 1966; Webb, 1968, 1977, 1991; Lebrun, 1971; Luxton, 1972, 1979;

Webb & Elmes, 1972; Anderson, 1975; Cancela da Fonseca, 1975; Jeuniaux & Moreau-Collinet, 1975; Stefaniak & Seniczak, 1976; Crossley, 1977; Cromack *et al.*, 1977; Schatz, 1979; Behan-Pelletier & Hill, 1983; Guegamian *et al.*, 1984; Siepel & de Ruiter-Dijkman, 1993; Siepel, 1994) the aim of the experiments described was to compare and to quantify their feeding activity in the presence of different food materials, mainly the white-rot fungi (Basidiomycetes) under the form of either their mycelium or the beech leaves (litter) already starting to be decomposed by them. Thus, their observed food preferences defined, as was expected (Luxton, 1972), their trophic behaviour, macrophytophage for *S. magnus*, panphytophage for *A. coleoptrata* and microphytophage for *D. verticillipes*.

Thus, the first results of the experiments conducted can be considered as a contribution to explain the macrotrophic behaviour of the three species of oribatid mites.

The preference of *S. magnus* for the bleached leaves and the leaves decomposed by the fungi corresponds to the species' aversion of lignin and polyphenols and to its low attraction to the mycelium of fungi, as already observed by Anderson (1973a, 1973b). This preference could reach about 6-7 times more than that for the

Table 7. – Average quantity of food material, in percent, consumed per week by three oribatid mites, *Steganacarus magnus*, *Achipteria coleoptrata* and *Damaeus verticillipes*, reared in the laboratory, after one week, one month and three months.

Food material	Average quantity of food material					
	Mean per week			Difference-rate per week		
	1 week	1 month (4 weeks)	3 months (12 weeks)	1 week	1 month-1 week (3 weeks)	3 months-1 month (8 weeks)
			Steganacarus magnus			
S01 (FSY)	1.64	2.43	1.10	1.64	2.69	0.44
S02 (cellulose)	2.20	1.88	1.13	2.20	1.14	0.76
S03 (polyphenols)	0.87	0.78	0.68	0.87	0.74	0.64
S05 (FTS)	0.49	0.86	–	0.49	0.99	–
S06 (SPU)	1.30	1.10	0.56	1.30	1.13	0.30
S07 (FSY + FTS:1w)	1.27	3.25	1.76	1.27	3.91	1.01
S08 (FSY + FTS:1m)	4.45	4.68	1.96	4.45	4.75	0.60
S09 (FSY + SPU:1w)	1.49	2.49	1.25	1.49	2.82	0.63
S10 (FSY + SPU:1m)	1.04	2.60	0.98	1.04	3.12	0.18
S11 (FSY + NaClO:2h)	2.11	2.63	1.20	2.11	2.80	0.49
S12 (FSY + NaClO:16 h)	5.74	5.35	2.51	5.74	5.22	1.09
			Achipteria coleoptrata			
S01 (FSY)	2.37	5.05	2.09	2.37	5.94	0.61
S02 (cellulose)	4.43	5.08	2.17	4.43	5.29	0.71
S03 (polyphenols)	5.06	5.58	2.07	5.06	5.75	0.31
S05 (FTS)	1.25	2.10	–	1.25	2.38	–
S06 (SPU)	3.20	2.85	1.42	3.20	2.73	0.70
S07 (FSY + FTS:1w)	3.30	2.88	1.28	3.30	2.73	0.49
S08 (FSY + FTS:1m)	3.50	3.28	1.45	3.50	3.20	0.54
S09 (FSY + SPU:1w)	2.57	3.30	1.44	2.57	3.54	0.51
S10 (FSY + SPU:1m)	2.35	2.34	1.00	2.35	2.33	0.33
S11 (FSY + NaClO:2h)	2.63	4.03	1.55	2.63	4.49	0.31
S12 (FSY + NaClO:16 h)	3.15	4.70	1.85	3.15	5.22	0.43
			Damaeus verticillipes			
S01 (FSY)	0	0.49	0.31	0	0.65	0.22
S02 (cellulose)	–	–	–	–	–	–
S03 (polyphenols)	0	0.55	0.32	0	0.73	0.21
S05 (FTS)	6.99	3.30	–	6.99	2.07	–
S06 (SPU)	4.96	2.60	0.93	4.96	1.81	0.10
S07 (FSY + FTS:1w)	0.92	1.44	0.50	0.92	1.61	0.04
S08 (FSY + FTS:1m)	2.77	2.83	–	2.77	2.84	–
S09 (FSY + SPU:1w)	4.04	2.28	0.94	4.04	1.69	0.28
S10 (FSY + SPU:1m)	3.28	3.13	1.06	3.28	3.07	0.03
S11 (FSY + NaClO:2h)	0	0.38	0.20	0	0.50	0.12
S12 (FSY + NaClO:16 h)	0	0.63	0.27	0	0.84	0.09

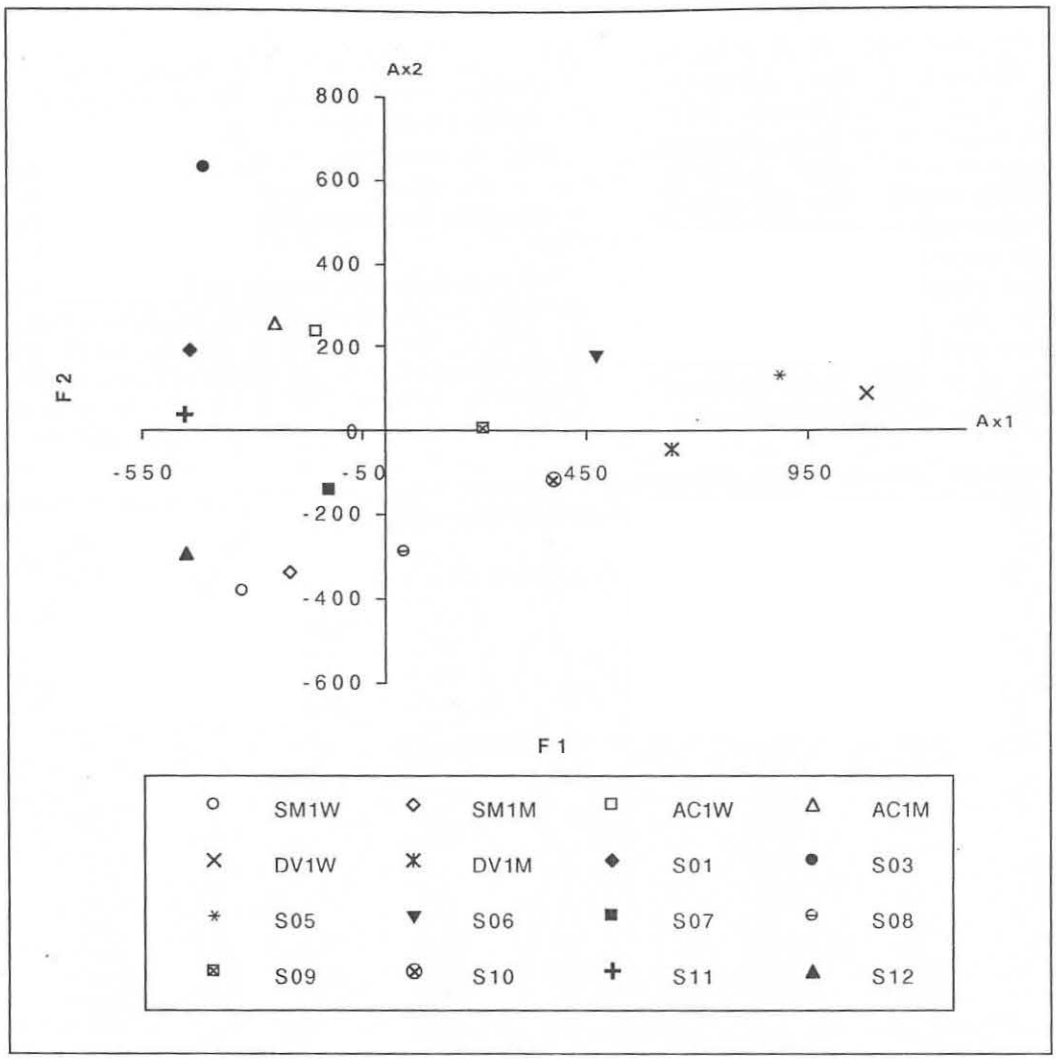

Figure 1. – Correspondence analysis: Species(3)-time(2) *versus* common food material(10). AC: *A. coleoptrata*; SM: *S. magnus*; DV: *D. verticillipes*; 1W: one week; 1M: one month; S01 to S12: substrates (see Material and Methods).

polyphenols and 9-12 times more than that for the mycelium (*table* 4). *S. magnus* is thus mainly a plant litter eater –macrophytophage– which is able to "digest plant structural material" (Webb, 1977) and consumes the parenchyma tissue of the leaves, leaving more or less intact their veins (Rihani, 1985). This behaviour is supported by the nature of its digestive enzymes (Luxton, 1972, 1979; Zinkler, 1971, 1972; Webb, 1977; Siepel & de Ruiter-Dijkman, 1993) and by laboratory and field experiments (Murphy, 1952, 1953; Berthet, 1964; Webb, 1968, 1977, 1991; Luxton, 1972; Webb & Elmes, 1972; Anderson, 1971, 1975; Cancela da Fonseca, 1975; Guegamian *et al.*, 1984; Rihani, 1985, 1988; Siepel & de Ruiter-Sijkman, 1993). A similar behaviour was observed by Hartenstein (1962a, 1962b) for another species of the same genus, *S. diaphanum* Jacot, which "would not feed on the lignin" and "rarely fed upon fungi not incorporated into leaves or wood". However, Behan-Pelletier & Hill (1983) having found in the guts of *S. magnus* fungi spores and animal fragments consider it as a panphytophage, though they suggest that these elements were the contaminants of their primary food source, the plant material.

On the contrary, *A. coleoptrata* clearly preferred either the leaves not attacked by white-rot fungi or mainly the leaf components (cellulose, polyphenols and to a lesser extent lignin as it was also observed by Stefaniak & Seniczak, 1976), to the leaves decomposed by white-rot fungi and to the leaves chemically bleached. This preference could attain a maximum of 2.4 times more (*table* 5). Nevertheless, the consumption of the last substrates indicated above and of the fungal mycelium is quite similar and high enough. Then, there are no clearly important differences concerning a particular food

item. According to Luxton (1972), though beech leaves can be occasionally eaten by *A. coleoptrata*, this species seems to be a "restricted feeder" as its carbohydrase enzymes complex is reduced, complex which is similar to that of the macrophytophages (Luxton, 1972, 1979; Siepel & de Ruiter-Dijkman, 1993). Lebrun (1971) and Schatz (1979) considered it a macrophytophage. However, even if this species seems to prefer leaf parenchyma in relation with the stage of leaf decomposition (Wallwork, 1958), fungal hyphae seem to be also a suitable diet (Wallwork, 1958; Farahat, 1966; Luxton, 1972; Stefaniak & Seniczak, 1976).

D. verticilippes consumed principally the white-rot fungi mycelium and spores developed either freely in culture or on the surface of leaves or inside them. This species not only consumed a very small amount of polyphenols and of leaves not attacked by the fungi or artificially bleached, but also survived rarely for more than one month on such substrates. Its mycophage behaviour was also observed by Schuster (1956), Cancela da Fonseca (1975) and Siepel & de Ruiter-Dijkman (1993).

This oribatid feeding behaviour concerning the leaves attacked by the white-rot fungi is a quite interesting differential point, particularly between *D. verticillipes* and *S. magnus*. The first species looks for hyphal fragments inside the leaves while the second looks, not for fungal mycelium, but for plant tissues with a low content of lignin and polyphenol due to the action of the white-rot fungi present. The position of *A. coleoptrata* seems to be intermediary, not too much doubt.

Although *S. magnus* preferred *S. pulverulentum* to FTS mycelium (twice on average), it consumed more leaves decomposed by FTS than by *S. pulverulentum* (maximum: 2.7 times more), which seems difficult to understand and in contradiction with what we know about the decomposing activity rate of the two fungi (Rihani *et al.*, in press). The same phenomenon was observed with *A. coleoptrata*, the average preference for *S. pulverulentum* mycelium being the same and that for the leaves decomposed by FTS being smaller, with a maximum of 1.5 times more. The situation with *D. verticillipes* is quite opposite to the other two species: preference for FTS mycelium (about 1.4 times more) and for leaves decomposed by *S. pulverulentum*, with a maximum of 2.6 times more. These differences should be investigated in further detail. We know that the enzyme structures of *S. magnus* and *A. coleoptrata* show slight differences (Luxton, 1972, 1979; Zinkler, 1972), and that *A. coleoptrata* shows a high cellulolytic activity (Luxton, 1972; Siepel & de Ruiter-Dijkman, 1993). On the other hand, Rihani (1988) and Rihani *et al.* (in press) have shown that the physiological activity of the two white-rot fungi studied is quite different. *S. pulverulentum* grows quickly and has a greater enzymatic activity than FTS. But, the gap between the rates of decomposition due to the two fungi is bigger concerning the cellulolytic activity and smaller concerning the ligninolytic activity, with the phenolytic activity in between. Can

Table 8. – Sign test analysis of the data of *table* 7, difference-rate per week. (N: number of pairs of food material; x: number of fewer signs, in each pair, either + or –; p: the distribution probability of +'s or –'s). – H0: The rate of food consumption is about the same in one or the other set (either time or species). H1: The rate of food consumption is higher in one set than in the other.

	Steganacarus magnus (SMA)			*Achipteria coleoptrata* (ACO)			*Damaeus verticillipes* (DVP)		
Items	1 week *vs* 1 month	1 week *vs* 3 months	1 month *vs* 3 months	1 week *vs* 1 month	1 week *vs* 3 months	1 month *vs* 3 months	1 week *vs* 1 month	1 week *vs* 3 months	1 month *vs* 3 months
N	11	10	10	11	10	10	10	8	8
x	4	0	0	4	0	0	4	4	0
p	0.274	0.001	0.001	0.274	0.001	0.001	0.377	0.637	0.004
Significance	n.s.	*	*	n.s.	*	*	n.s.	n.s.	*
H0-H1	1w = 1m H0	1w > 3m H1	1m > 3m H1	1w = 1m H0	1w > 3m H1	1m > 3m H1	1w = 1m H0	1w = 3m H0	1m > 3m H1

Items	*S. magnus* vs *A. coleoptrata*			*S. magnus* vs *D. verticillipes*			*A. coleoptrata* vs *D. verticillipes*		
	1 week	1 month	3 months	1 week	1 month	3 months	1 week	1 month	3 months
N	11	10	10	10	10	8	10	10	8
x	2	3	3	4	2	0	4	1	0
p	0.033	0.172	0.172	0.377	0.145	0.004	0.377	0.011	0.004
Significance	*	n.s.	n.s.	n.s.	n.s.	*	n.s.	*	*
H0-H1	SMA < ACO H1	SMA = ACO H0	SMA = ACO H0	SMA = DVP H0	SMA = DVP H0	SMA > DVP H1	ACO = DVP H0	ACO > DVP H1	ACO > DVP H1

Sign test: matching pairs (Siegel, 1956: p. 68, tab. D). Region of rejection of H0: $p = 0.05$. For $p < 0.05$, H0 is rejected. – H0: The median of the differences is zero, *i.e.* p (Xa > Xb) = p (Xa < Xb) = 1/2. H1: The median of the differences is positive.

these differences explain the feeding preferences? That is, the *S. magnus* preference for the leaves decomposed by FTS, the *A. coleoptrata* preference for the same type of leaves and also the leaves decomposed by *S. pulverulentum*, mainly during one week, as well as the *D. verticillipes* preference for the leaves decomposed by *S. pulverulentum*, which we assume have a greater density of hyphal fragments inside them?

Moreover, an interesting fact was revealed, the differential attraction of the three oribatids for the two white-rot fungi studied: *S. magnus* for *S. pulverulentum* mycelium but leaves decomposed by FTS; *A. coleoptrata* for *S. pulverulentum* mycelium and leaves decomposed by *S. pulverulentum*; and *D. verticillipes* for FTS mycelium but leaves decomposed by *S. pulverulentum*. This can be due to differences in food palatability, either litter (Murphy, 1954; Lebrun, 1971) or hyphae (Cancela da Fonseca, 1975). And it supports the hypothesis of a strong microtrophic specificity of the microarthropods towards the soil organic matter and microflora (Cancela da Fonseca & Poinsot-Balaguer, 1983; Cancela da Fonseca, 1988).

The second important set of results indicates the differential relationships between oribatids and white-rot fungi and the synergetic effects of that relation. Thus, *S. magnus* feeding behaviour shows that the effect of the attack of leaves by FTS, mainly during one month, increases consumption, as compared to the leaves not attacked and the leaves attacked by *S. pulverulentum* during one month, of about 2-3 times. In the case of *A. coleoptrata*, the most important effect of leaf decomposition by FTS is the difference between those leaves decomposed during one month by FTS and the leaves decomposed also during one month but by *S. pulverulentum*: 1.5 times more. The relationship of leaves not attacked by the fungi and the leaves decomposed by them is inverse to that of the *S. magnus*: the consumption of the leaves not attacked by the fungi varies between 1.2 and 1.8 times more. Finally, for *D. verticillipes* it is the consumptions of leaves attacked by *S. pulverulentum*, either during one week or one month, that are higher than those attacked by FTS: they vary between 1.2 and 2.6 times more.

Thus, the association between oribatid mites and white-rot fungi increases the consumption rate of the beech leaves (litter) and, in that way, the

Table 9. – Relative proportion of the feeding rates (> 1.0) of the three species of oribatid mites, specially in relation with the significance obtained through ANAFAC analysis (+) (cf. *table* 10).

	Steganacarus magnus (*SMA*)			*Achipteria coleoptrata* (*ACO*)			*Damaeus verticillipes* (*DVP*)		
Food material	1 week	1 month	3 months	1 week	1 month	3 months	1 week	1 month	3 months
S01	–	–	–	1.5 *SMA*$^+$	2.1 *SMA*$^+$	1.9 *SMA*$^+$	–	–	–
(FSY)	∞ *DVP*	5.0 *DVP*	3.6 *DVP*	∞ *DVP*	10.4 *DVP*$^+$	6.8 *DVP*	–	–	–
S02	–	–	–	2.0 *SMA*	2.7 *SMA*	1.9 *SMA*	–	–	–
(cellulose)	–	–	–	–	–	–	–	–	–
S03	–	–	–	5.8 *SMA*$^+$	7.2 *SMA*$^+$	3.0 *SMA*	–	–	–
(polyphenols)	∞ *DVP*	3.4 *DVP*	2.1 *DVP*	∞ *DVP*	10.1 *DVP*	6.4 *DVP*	–	–	–
S05	–	–	–	2.6 *SMA*	2.4 *SMA*$^+$	–	14.3 *SMA*$^+$	3.8 *SMA*$^+$	–
(FTS)	–	–	–	–	–	–	5.6 *ACO*$^+$	1.6 *ACO*$^+$	–
S06	–	–	–	2.5 *SMA*	2.6 *SMA*$^+$	2.5 *SMA*	3.8 *SMA*$^+$	2.4 *SMA*$^+$	1.7 *SMA*
(SPU)	–	–	–	–	1.1 *DVP*	1.5 *DVP*	1.6 *ACO*	–	–
S07	–	1.1 *ACO*	1.4 *ACO*	2.6 *SMA*	–	–	–	–	–
(FSY + FTS:1w)	1.4 *DVP*$^+$	2.3 *DVP*$^+$	3.5 *DVP*	3.6 *DVP*$^+$	2.0 *DVP*$^+$	2.6 *DVP*	–	–	–
S08	1.3 *ACO*$^+$	1.4 *ACO*$^+$	1.4 *ACO*$^+$	–	–	–	–	–	–
(FSY + FTS:1m)	1.6 *DVP*$^+$	1.7 *DVP*$^+$	–	–	–	–	–	–	–
S09	–	–	–	1.7 *SMA*$^+$	1.3 *SMA*$^+$	1.2 *SMA*$^+$	2.7 *SMA*	–	–
(FSY + SPU:1w)	–	1.1 *DVP*	1.3 *DVP*	–	1.5 *DVP*$^+$	1.5 *DVP*	1.6 *ACO*	–	–
S10	–	1.1 *ACO*	–	2.3 *SMA*	–	–	3.2 *SMA*	1.2 *SMA*	1.1 *SMA*
(FSY + SPU:1m)	–	–	–	–	–	–	1.4 *ACO*	1.3 *ACO*$^+$	1.1 *ACO*
S11	–	–	–	1.3 *SMA*	1.5 *SMA*	1.3 *SMA*	–	–	–
(FSY + NaClO:2h)	∞ *DVP*	7.0 *DVP*	5.8 *DVP*	∞ *DVP*	10.3 *DVP*	7.7 *DVP*	–	–	–
S12	1.8 *ACO*$^+$	1.1 *ACO*$^+$	1.4 *ACO*	–	–	–	–	–	–
(FSY + NaClO:16 h)	∞ *DVP*	8.5 *DVP*	9.3 *DVP*	∞ *DVP*	7.4 *DVP*$^+$	6.9 *DVP*	–	–	–

potential rate of decomposition of them. Rihani (1985) has implicitly observed this phenomenon. Based on his data, we have calculated that the consumption, during one month, of the beech leaves by *S. magnus* alone was about 8% of their initial dry weight compared with the 24% decomposition by the sole FTS. When the oribatid ate the leaves already decomposed by this fungus, the consumption increased to 37%. Guegamian *et al.* (1984) have shown that the association of *S. magnus* with an aerobic cellulolytic bacterium, *Sporocytophaga myxococcoides* (Krz.) Stanier, increased its consumption of the beech leaves by 1.2 times the consumption of the oribatid alone and by 3.4 times the decomposition activity of the sole bacteria. Furthermore, its association with the total soil microflora increased its consumption by 1.3 times the action of the oribatid and by 1.9 times the sole action of the total soil microflora. The synergetic action of the microarthropods on litter decomposition has been indicated already by Kurcheva (1960) and Crossley & Witkamp (1964). Nevertheless, to evaluate the real importance of these soil organisms (oribatids and microflora) on the total degradation of organic matter, it will be necessary: (a) for the fauna, to deduct the faecal pellets from the weight of the organic matter not decomposed, and, (b) for the microflora, to add these same pellets which are going to be decomposed by them afterwards (Guegamian, *et al.*, 1984). Rihani (1985) obtained from appropriate cultures of *S. magnus* faecal pellets, fungal colonies, principally of *Penicillium* spp., with bacteria and sometimes white-rot fungi. Furthermore, ultrastructural analysis of these pellets has shown that plant fragments, hyphae and spores are closely mixed up with bacteria. However, several authors indicated that in their pellets they found mostly leaf particles and few fungal hyphae (Spencer, 1951; Murphy, 1955; Hayes, 1963; Anderson, 1971), which agree with their gut contents (Siepel & de Ruiter-Dijkman, 1993).

In their review of the feeding habits of soil microarthropods, Cancela da Fonseca & Poinsot-Balaguer (1983) suggested that these habits must be defined more in relation to a trophic specificity (microtrophism) than to a macroscopic trophic behaviour (macrotrophism), *i.e.* each species can be polyphagous in relation to the ingested food but monophagous in relation to a key-substance.

In 1993, Siepel & de Ruiter-Dijkman defined the feeding guilds of oribatid mites in almost the same way, though only the activity of the carbohydrase enzymes were taken into account: (a) cellulase, which digest the cellulose, a component of the cell-walls of the green plants; (b) chitinase, which digest the chitin, a component of the fungal cell-walls; and (c) trehalase, which digest the trehalose, a component of the fungal cell-contents.

Table 10. – Relative importance of the three species of oribatid mites *S. magnus* (SMA), *A. coleoptrata* (ACO) and *D. verticillipes* (DVP) in relation to the different sets of food material analysed and to their differential attributes, expressed in terms of the contribution to the definition of the factors (axes) obtained by different correspondence analyses (ANAFAC).

ANAFAC analyses (code)	Species	Food material (number)	Time of food consumption (weeks, months)	Factors (axes, contri-butions)	Species Contributions		Food material Contributions		Differential attributes
					(axis side +)	(axis side –)	(axis side +)	(axis side –)	
SAD1	SMA	S01, S03	1w, 1m	Ax1	DVP-1m	ACO-1m	S05	S01, S12	FST*vs* FSY &
	ACO	S05-S12		C1	40%	13%	36%	10%, 15%	FSY + NaClO:16h
	DVP	(10)		Ax2	ACO-1m	SMA-1m	S03	S08, S12	Polyphenols *vs* FSY + FTS:1m
				C2	36%	45%	50%	17%, 17%	& FSY + NaClO:16h
				Ax3	DVP-1w	ACO-1w	S05	S07	FTS *vs* FSY + FTS:1w
				C3	29%	18%	14%	30%	
SAD5	SMA	S05-S10	1w, 1m	Ax1	DVP-1m(1w)	SMA-1m(1w)	S05, S06	S07, S08	FTS & SPU *vs* FSY + FTS:1w
	ACO	(6)		C1	19%(+35%)	39%(+6%)	47%, 11%	21%, 21%	& FSY + FTS:1m
	DVP			Ax2	DVP-1m	ACO-1m	S10	S07, S09	FSY+SPU:1m *vs* FSY+FTS:1w
				C2	18%	42%	10%	21%, 11%	& FSY + SPU:1w
SA1	SMA	S01-S03	1w, 1m	Ax1	ACO-1m(1w)	SMA-1m(1w)	S03	S08, S12	Polyphenols *vs* FSY + FTS:1m
	ACO	S05-S12		C1	34%(+6%)	50%(+9%)	18%	20%, 17%	& FSY + NaClO:16h
		(11)							
SA3	SMA	S01	1w, 1m	Ax1	ACO-1m	SMA-1m	S01, S05, S06	S08	FSY & FTS & SPU *vs*
	ACO	S05-S10		C1	47%	44%	26%, 16%, 15%	40%	FSY + FTS:1m
		(7)							
SA5	SMA	S01	1w, 1m, 3m	Ax1	ACO-1m, 3m	SMA-1m, 3m	S01	S08	FSY *vs* FSY + FTS:1m
	ACO	S07-S10		C1	26%, 26%	18%, 22%	58%	30%	
		(5)							
SA6	SMA	S07-S10	1w, 1m, 3w	Ax1	ACO-1m, 3m	SMA-1w, 1m	S09	S08	FSY + SPU:1w *vs*
	ACO	(4)		C1	18%, 21%	39%, 16%	38%	57%	FSY + FTS:1m

Thus, *S. magnus* and *A. coleoptrata*, having only cellulase activity, are herbivorous grazers, *i.e.* they "are able to feed on both the green plants cell-contents and cell-walls" (a part of Luxton's macrophytophage), and *S. verticillipes*, having chitinase activity as well as trehalase activity, is a fungivorous grazer, *i.e.* able to feed on both the fungal cell-walls and cell-contents (a part of Luxton's microphytophages).

The food preferences of each species as well as its ability to digest them are then important components of the ecological niche of the species (Cancela da Fonseca, 1987; Siepel, 1990).

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